ORIGINAL PAPER

Application of bomb radiocarbon chronologies to shortfin mako (*Isurus oxyrinchus*) age validation

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Abstract Age estimation is an issue for the shortfin mako, *Isurus oxyrinchus*, because of disagreement on vertebral band-pair deposition periodicity. In the 1950s–1960s, thermonuclear testing released large amounts of radiocarbon into the atmosphere, which diffused into the ocean through gas exchange. This influx created a time-specific marker that can be used in age validation. Annual band-pair deposition in the porbeagle, *Lamna nasus*, was validated in a previous study and indicated preliminary annual deposition in the shortfin mako, using four samples from one vertebra. In the present study, age estimates from 54 shortfin mako vertebrae collected in 1950–1984 ranged 1–31 years. Ageing error between readers was consistent, with 76% of the estimates ranging within 2 years. Twenty-one $\Delta^{14}C$ values from eight shortfin mako vertebrae (collected in the western North Atlantic in 1963–1984) ranged –154.8‰ to 86.8‰. The resulting conformity with the $\Delta^{14}C$ timeline for the porbeagle supported annual band-pair deposition in vertebrae of the shortfin mako.

Keywords Shark vertebrae · Lamnidae · Band pairs · Growth

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Introduction

There is an ongoing disagreement regarding the ageing of the shortfin mako due to a difference of interpretation in the periodic deposition of vertebral growth band pairs, especially for the larger size classes. Pratt and Casey (1983), using analysis of length-month information, tagging data, and length-frequency analysis, concluded that two band pairs were formed in the vertebral centrum every year (biannual band-pair interpretation). Cailliet et al. (1983), however, presented growth parameters based on the common assumption that one band pair forms annually (annual band-pair interpretation). Therefore, growth rates

obtained by Pratt and Casey (1983) were twice that of Cailliet et al. (1983) and could lead to age discrepancies of about 15 years for maximum estimated ages on the order of 30 from the annual band-pair interpretation.

Serious consequences in the population dynamics could occur for this species if inputs are based on an invalid age interpretation. The latest Fishery Management Plan (FMP) for Highly Migratory Species (HMS), for example, adopted the biannual band-pair deposition hypothesis because it apparently fit the observed growth patterns best (Pacific Fishery Management Council 2003). However, the ongoing uncertainty about the ageing of the shortfin mako was acknowledged and it was recommended that an endeavor to resolve this issue be made.

Since 1983, five additional studies on the age and growth of the shortfin mako have been conducted (Chan 2001; Campana et al. 2002; Hsu 2003; Ribot-Carballal et al. 2005; Bishop et al. 2006). Using Marginal Increment Ratio (MIR), Hsu (2003) indicated the formation of annual translucent bands from July to September in western North Pacific Ocean shortfin makos. Using Marginal Increment Analysis (MIA) Ribot-Carballal et al. (2005) supported the annual band-pair interpretation for 109 shortfin makos collected in the eastern Pacific Ocean. Although the study provided support for annual band-pair deposition, no statistical test was performed and the number of samples for MIA analysis was insufficient for some months. Hence, unequivocal validation of shortfin mako age estimates has yet to be accomplished.

Atmospheric testing of thermonuclear devices in the 1950s and 1960s effectively doubled the natural atmospheric radiocarbon (^{14}C; Druffel and Suess 1983; Broeker et al. 1985). The elevated ^{14}C levels were first recorded in 1957–1958, with a peak around 1963 (Nydal and Lovseth 1983). As a consequence, ^{14}C entered the ocean through gas exchange with the atmosphere at the ocean surface and in terrestrial runoff (Broeker et al. 1985). Despite variable oceanographic conditions, a worldwide rise of the bomb ^{14}C signal entered the ocean mixed layer as dissolved inorganic carbon (DIC) in 1957–1958 (Druffel 1980). The large amounts of ^{14}C released from the

bomb tests produced a signature that can be followed through time, throughout the marine food web, and into deeper waters (Pearcy and Stuiver 1983). The marked increase of radiocarbon levels was first measured in the DIC of seawater and in biogenic marine carbonates of hermatypic corals in Florida (Druffel and Linick 1978). Subsequently, this record was documented in corals from other regions (e.g. Nozaki et al. 1978; Druffel 1980; Druffel and Suess 1983; Druffel 1989; Guilderson et al. 1998) and in the thallus of rhodoliths (Frantz et al. 2000, 2005). The accumulation of radiocarbon in the hard parts of most marine organisms in the mixed layer (such as fish otoliths and bivalves) was synchronous with the coral time-series (Kalish 1993; Weidman and Jones 1993).

This technique has been used to validate age estimates and longevity of numerous bony fishes to date, as well as to establish bomb radiocarbon chronologies from different oceans (e.g. Kalish 1993; Campana 1997; Campana and Jones 1998; Piner and Wischniowski 2004; Andrews et al. 2005; Kerr et al. 2005). In the first application of this technique to lamnoid sharks, Campana et al. (2002) validated annual band-pair deposition in vertebral growth bands for the porbeagle, *Lamna nasus*, aged up to 26 years. Radiocarbon values from samples obtained from 15 porbeagle caught in the western North Atlantic Ocean (some of which were known-age) produced a chronology similar in magnitude to the reference carbonate chronology for that region. The observed phase shift of about 3 years was attributed to different sources of carbon between vertebrae and those for otoliths, bivalves and corals. In the same study by Campana et al. (2002), a single vertebra from a shortfin mako caught in 1977 was aged at 21 and 10 years, using the annual versus the biannual deposition hypotheses, respectively. Vertebral samples were extracted from the first, last, and two intermediate bands and were assayed for radiocarbon. The results indicated the ageing interpretation for the vertebra from this fish best fit the timing of the porbeagle time-series by adopting the annual band-pair interpretation.

To provide a more comprehensive basis for valid ageing criteria and a definitive growth function for the shortfin mako, more radiocarbon

assays were required (Campana et al. 2002). The goal of our research was to take heed of this suggestion and continue the use of bomb radiocarbon to validate the ageing of the shortfin mako, and specifically to resolve the validity of either annual or biannual band-pair age interpretations.

Materials and methods

Age assessment

Vertebral samples were collected from shortfin makos caught in the western North Atlantic, eastern North Pacific, western South Pacific, and western South Indian Oceans between 1950 and 1984 to obtain sufficient sample size across size classes. These centra were sectioned for age estimation using the growth bands visible in the corpus calcareum, an approach commonly used in shark age estimation. Each vertebral centrum was sectioned along the sagittal plane using a Ray Tech gem saw with two diamond blades separated by a 0.6 mm spacer at the NOAA Fisheries Northeast Fisheries Science Center, Narragansett Laboratory, Rhode Island (NMFS). The resulting sections were placed under water with a black background and digitally photographed using an MTI® CCD 72 video camera mounted on an Olympus® SZX9 stereomicroscope under reflected light. Magnification ranged between 4× and 12× according to the size of the vertebra. For larger vertebrae, an additional photograph at higher magnification was taken to resolve the finer bands toward the edge. The sections were stored in 70% EtOH.

Ages were estimated by counting the number of band pairs in the images using the annual band-pair interpretation. Brightness and contrast of the images was adjusted to enhance the banding pattern of the section using Adobe Photoshop 7.0. Each band pair consisted of one opaque and one translucent band, corresponding to the light-dark pattern observed against a dark background under reflected light.

Vertebrae were independently aged by a second reader at the NMFS Narragansett lab to assess reading precision and for cross-calibration between readers. Age discrepancies were plotted to show the age difference frequency between readers. An age-bias plot was produced to detect bias among the size range and to suggest trends in this type of error. In addition, Average Percent Error (APE), Percent Error (D) and Coefficient of Variation (CV) were calculated to measure precision of the readings (Beamish and Fournier 1981; Chang 1982; Campana 2001). The resulting CV was used as a measure of the potential age range in the assigned year of formation for the samples assayed for radiocarbon. Because the uncertainty in assigning the year of formation decreased from the first-formed band to the last-formed band (where the collection date was known), the closer the sample to the band pair corresponding to the year of collection, the smaller the error and vice versa. Hence, the effect of this uncertainty increased as the samples approached the birth year. Individual CV values for each sample were calculated multiplying the difference between the collection year and the year of band-pair formation by CV.

Sample preparation

To address the validity of age interpretations, samples for radiocarbon analysis were extracted from growth bands of specimens collected from the western North Atlantic Ocean with estimated collection years between 1963 and 1984. The sharks were from the same collection as those used by Campana et al. (2002). To avoid the use of vertebrae sectioned for ageing, adjacent vertebrae were sectioned along the sagittal plane to a thickness of 1.3 mm using a Buehler Isomet® 1000 low-speed saw with a diamond blade. Samples corresponding to specific years of formation were extracted from the center of growth bands using a New Wave Research® Micromill with Brasseler® Carbide tips (0.3 mm). The drill bits were rinsed in 10% HCl and MilliQ water between sampling events to prevent cross-contamination. Vertebral sections were mounted for milling using double-sided tape and samples were extracted by drilling a series of holes along the boundary of the two growth bands. The extracted samples were solid pieces composed of one opaque and one translucent band, corresponding to

what would be interpreted as one year of growth, based on the annual band-pair interpretation, or half a year's growth, based on the biannual band-pair interpretation. Samples were weighed to the nearest 0.1 mg and placed in glass culture tubes (13×100 mm) for processing prior to radiocarbon analysis. For all but one specimen, the first-formed band pair and a series of other growth band pairs ranging to the most recently formed were extracted from the corpus calcareum of each vertebral section. Four of these samples were cored from vertebrae belonging to the same shortfin mako assayed by Campana et al. (2002) to provide a basis for direct comparisons.

Prior to radiocarbon analysis, samples were demineralized to remove any carbon bound into what could be more transient carbonate forms. This step was necessary to attribute all carbon, and measured ^{14}C, to the organic component of the cartilage. To demineralize the sample, culture tubes containing the samples were filled half way with 0.25 N HCl (GFS Chemicals, double distilled acid); acidified samples were capped with foil and placed in a refrigerator for 2 h to slow the reaction (Brown et al. 1988). Hydrochloric acid was drawn off with a pipette from the remaining solid sample, leaving the extracted piece of cartilage at the bottom of the tube; the tubes were re-filled with fresh acid and placed in a refrigerator overnight to complete the dissolution of the inorganic component.

Demineralization was considered complete once the solid material appeared translucent. Samples were rinsed, centrifuged, and transferred into pre-weighed 6 mm quartz tubes. Samples were dried overnight at 95°C and weighed. Dried samples were prepared for combustion by adding the equivalent of 20 times the sample weight in Alpha Aesar® CuO (99.9999%) and 2 mg of Alpha Aesar® Ag (99.999% metals basis). Tubes were evacuated and sealed, placed in an oven at 900°C for 3.5 h and analyzed for $\Delta^{14}C$ by Accelerator Mass Spectrometry (AMS).

Bomb radiocarbon dating

The $\Delta^{14}C$ values from each sample were plotted against the year of band formation based on estimated age and compared to reference time-series obtained from the western North Atlantic for the porbeagle by Campana et al. (2002), the haddock *Melanogrammus aeglefinus* (Campana 1997), and the bivalve *Arctica islandica* (Weidman and Jones 1993). Results from the shortfin mako bomb carbon analysis were expected to produce a sigmoidal curve similar to the three $\Delta^{14}C$ time-series from the western North Atlantic Ocean. A phase lag was defined as a shift in time of onset and increase between chronologies. $\Delta^{14}C$ values were subjectively considered elevated when above 30‰.

To verify the synchrony of the onset and increase of the bomb radiocarbon signal within individual sharks, sequential samples obtained from each specimen were plotted with those from the porbeagle chronology. Differences in timing of the bomb radiocarbon signal observed when the two different ageing interpretations were applied, radiocarbon values from samples of the two longest-living specimens available (life span from pre- to the post-bomb era) were also plotted with the reference time-series. To provide the best analysis using known-age samples for the shortfin mako, samples from the edge of the vertebrae were plotted with the porbeagle reference time-series. The resulting time-series was used to verify the presence of the bomb radiocarbon signal. These values served also as a reference time-series for the shortfin mako because the year of formation was known or had little uncertainty.

Results

Age estimates for the 54 shortfin mako vertebrae ranged from 1 years to 31 years, using the annual band-pair interpretation. Estimated birth years for those samples spanned from 1948 to 1972, covering the period of the bomb radiocarbon increase. If the biannual band-pair interpretation was used, the age range would be reduced to 1–15 years with corresponding birth years between 1957 and 1978. Vertebral growth bands in the early life stages of shortfin mako sharks appeared broad and clear, as shown in transverse section; however, the bands became narrower and less defined, often blending with other bands, as age increased (Fig. 1).
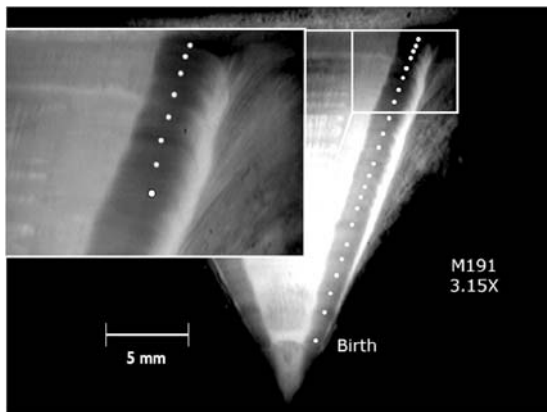
Fig. 1 Transverse section of a vertebra (M191) from a 350-cm (TL) shortfin mako shark collected in 1979 and aged at 22 years. Each dot is centered on the opaque region of a band pair, but represents one whole year of growth. Age 0+ was assigned to the first-formed band (marked as Birth)

Band-pair counts remained consistent between two readers and showed no ageing bias throughout the available size range (Fig. 2). Comparison of age estimates with the second reader yielded an APE value of 11.5% and D value of 7.7%. The CV of 10.8% was used as a measure of the potential age range in the assigned year of formation for the samples assayed for radiocarbon.

The vertebrae of two male and six female shortfin makos, (133–366 cm TL), were analyzed for ^{14}C, producing a total of 21 samples (Table 1). Collection dates ranged from 1963 to 1984. Ages

of the selected specimens, adopting the annual band-pair criteria, were estimated at 2–31 years with corresponding birth years of 1948–1972. The error associated with assigned year of band-pair formation for each sample (CV) ranged between 0.1 years and 3.3 years.

For the samples assayed, radiocarbon values for 21 samples ranged between –154.8‰ (±3.2 SD) and 86.8‰ (±4.6) Δ^{14}C and were estimated to have formed between 1948 and 1983, using the annual band-pair interpretation. The lowest value (–154.8‰ ± 3.2) corresponded to the estimated year 1957; the highest values (86.5‰ ± 4.8 and 86.8‰ ± 4.6) corresponded to the estimated years 1968 and 1978, respectively. Radiocarbon values of shortfin mako vertebrae, relative to their estimated year of band-pair formation, revealed the presence of a bomb radiocarbon signal and followed the general predicted trend (Fig. 3). The resulting chronology was comparable to existing reference time-series of the North Atlantic Ocean. The phase lag of the rise in Δ^{14}C levels toward more recent dates, however, was most similar to the porbeagle and the increase in started as early as 1960, whereas the first elevated values for the shortfin mako were recorded between 1962 and 1968. The most elevated radiocarbon values for the shortfin mako were 86.5‰ ± 4.8 (1968) and 86.8‰ ± 4.6 (1978), whereas those for the haddock (Campana 1997) and the porbeagle (Campana et al. 2002) were 75‰ (1970) and 63‰ (1975), respectively.

Fig. 2 Age-bias plot showing inter-reader comparison, Average Percent Error (APE), Percent Error (D), and Coefficient of Variation (CV) ($n = 53$). Vertical error bars represent 95% Confidence Interval (CI). The unusually long bars for years 9, 13 and 21 are due to small sample size of the pair-wise comparisons for those year classes
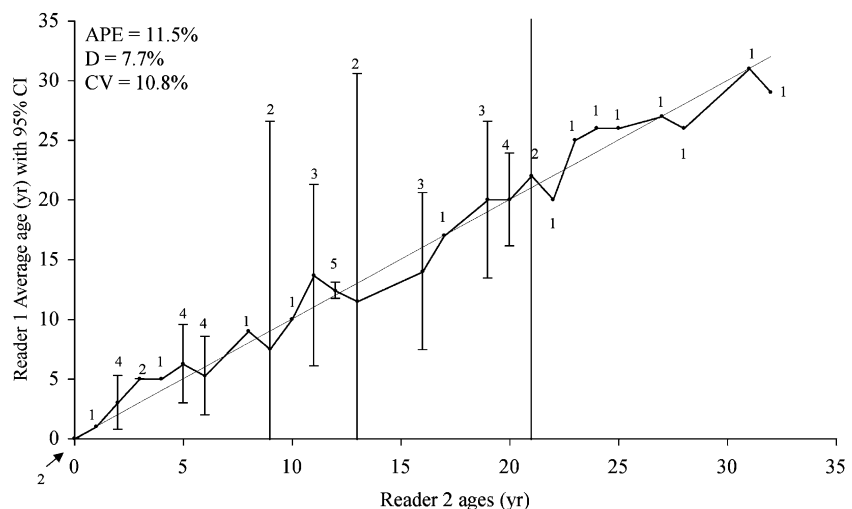
Table 1 Summary of fish and sample data for vertebral sections that were analyzed for $\Delta^{14}C$

Sample	Sex	TL (cm)	Collection date	Estimated age (years)	Estimated birth date	Estimated year of band-pair formation	Estimated age at band-pair formation	CV of assigned year of band-pair formation[a]	Sample weight (mg)[b]	$\Delta^{14}C$(‰)	±SD	$\partial^{13}C$ (‰)[c]
M001	F	133	1965	2	1963	1963	0+	0.2	17.1	−144.0	3.3	−15
M011	M	232	1963	13	1950	1950	0+	1.4	22.2	−69.8	4.4	−15
						1955	5	0.9	21.1	−132.7	4	−15
						1962	12	0.1	18	−50.6	3.7	−14
M016	M	183	1964	5	1959	1961	2	0.3	20	−69.4	3.6	−15
						1963	4	0.1	19	−51.9	3.6	−15
M151	F	355	1977	21	1956	1956	0+	2.3	20.2	−73.3	4.0	−15
						1956	**0+**			**−100.2**		
						1960	**4**			**−90.1**		
						1965	9	1.3	21.7	−64.2	3.6	−15
						1968	14	0.8	21.3	−45.8	4.6	−15
						1970	**16**			**38.8**		
						1976	20	0.1	20	64.0	5.2	−15
						1977	**21**			**52.6**		
M181	F	240	1979	11	1968	1968	0+	1.2	16	86.5	4.8	−14
						1972	4	0.8	20	35.6	4.1	−14
M186	F	366	1979	31	1948	1948	0+	3.3	16.1	−63.1	3.8	−15
						1955	7	2.6	18	−75.3	3.9	−15
						1966	18	1.4	18	−65.9	4.5	−14
						1978	30	0.1	20	86.8	4.6	−15
M191	F	350	1979	22	1957	1957	0+	2.4	21	−154.8	3.2	−15
						1962	5	1.8	15	−20.8	5.4	−15
						1966	9	1.4	21	−36.9	3.7	−15
M316	F	309	1984	12	1972	1972	0+	1.3	20	62.8	4.7	−15
						1983	11	0.1	20.5	58.0	4.3	−15

Age estimates were based on the annual deposition of one band pair per year. Values in bold represent the four vertebral samples assayed by Campana et al. (2002)

[a] CV = 10.8%

[b] Pre-demineralization

[c] $\partial^{13}C$ values are the assumed values according to Stuiver and Polach (1997)

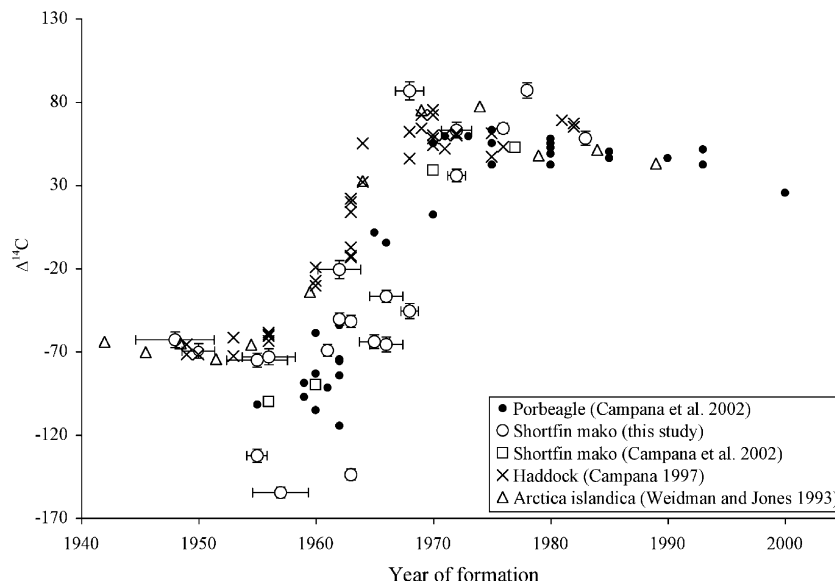**Fig. 3** Values of $\Delta^{14}C$ from individual growth band pairs of shortfin mako vertebrae collected from the western North Atlantic and plotted with the reference time series available from the same region, with the single shortfin mako previously assayed by Campana et al. (2002). The estimated years of formation were based on the annual band-pair interpretation. Horizontal error bars represent uncertainty associated with age estimation from growth bands (CV = 10.8%). Vertical bars represent the 1 SD AMS analytical uncertainty

Some $\Delta^{14}C$ values were lower than other pre-bomb values for the shortfin mako (>50‰) and the reference time-series. Depleted radiocarbon levels were found in the first-formed band pair of two specimens (M001 and M191) and in an intermediate band pair of another (M011). These values ranged between –132.7‰ ± 4 SD and –154.8‰ ± 3.2 SD and were estimated to have formed in 1955 (±0.9 years), 1957 (± 2.4 years), and 1963 (±0.2 years).

Within-shark vertebral analysis suggested that radiocarbon levels within individual sharks followed the same trend (Fig. 4). Bomb radiocarbon values obtained from sequential samples of the oldest sharks used in this study (M151 and M186) indicated the sharks began life in the pre-bomb phase, continued to live through the sharp increase in radiocarbon and into the post-bomb phase. All samples from those specimens tended to agree with the expected bomb radiocarbon trend. Some samples showed a phase lag of about 3–5 years relative to the porbeagle chronology for a total lag of 6–8 years relative to more synchronous records. The remainder was in phase with the porbeagle time-series. The most evident shift

from the expected trend appeared in four individual samples from three different specimens (M151-1965, M151-1968, M186-1966, and M191-1966) assumed to have formed between 1965 and 1968, during the rapid increase of radiocarbon levels. These samples were collected from growth bands formed at ages estimated between 9 years and 18 years, based on annual deposition.

There was a measurable discrepancy in radiocarbon values for one growth band between the present study and that reported by Campana et al. (2002) (circled samples, Fig. 4). A difference of 26.9‰ was recorded between values from samples from the first-formed band of a specimen (M151) sampled in Campana et al. (2002) and the present study. These samples were similar by location on the vertebral column, location in the centrum and estimated age, but were not replicates. Application of the two age interpretations to the two largest specimens, which were estimated to span throughout the bomb ^{14}C era, revealed two different scenarios (Fig. 5). Using data from M151 and M186, the initial rise and subsequent peak of the bomb radiocarbon levels differed markedly when applying the annual
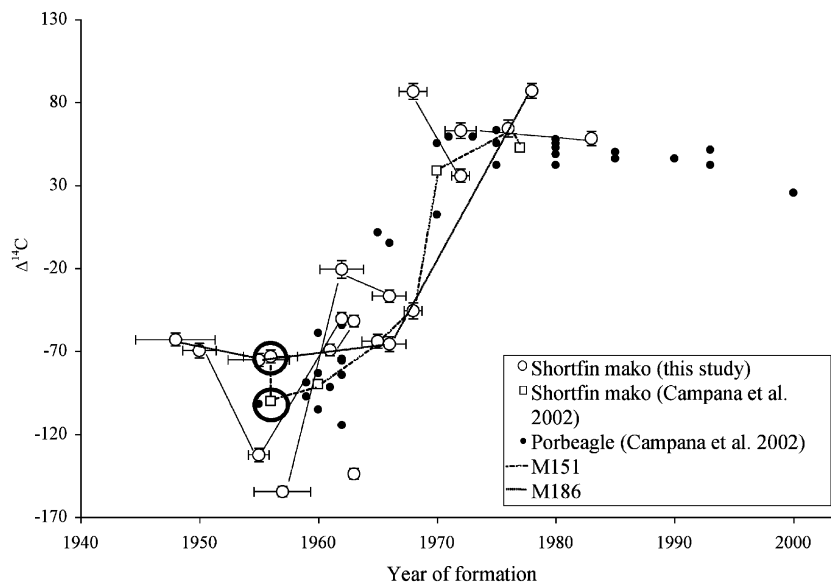
Fig. 4 Radiocarbon values from sequential samples (of vertebral growth bands) in individual sharks. Each line connects growth bands sampled from the same specimen and is plotted with the porbeagle time-series (Campana et al. 2002). The estimated years of formation of the sampled bands used the annual band-pair interpretation. Circles highlight values from the first-formed band pair assayed both in this study and that by Campana et al. (2002) for M151. Horizontal error bars represent uncertainty associated with age determination from growth zones (CV = 10.8%). Vertical bars represent the 1 SD AMS analytical uncertainty

Fig. 5 Radiocarbon values for two individual shortfin makos versus the estimated year of formation as the result of two growth band interpretations. Solid lines connect sequential sampling from specimens aged using the annual band-pair interpretation. Dotted lines connect sequential growth bands of specimens aged using the biannual band-pair interpretation
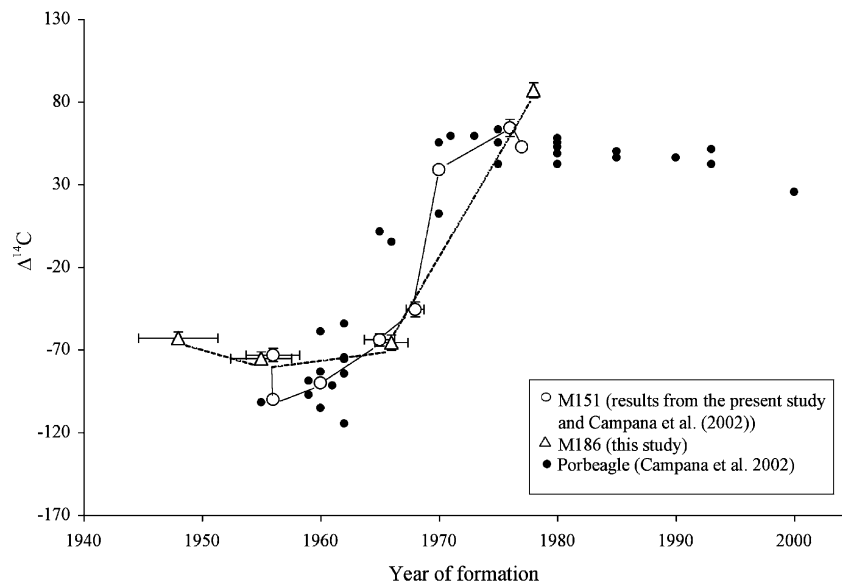
versus biannual band-pair deposition hypotheses. The outcome was an apparent 3–5 years of lag relative to the porbeagle chronology with the annual band-pair interpretation. The phase lag would be 10–13 years relative to the porbeagle for this interpretation to be valid. The biannual band-pair interpretation resulted in time series that indicated the first effects of the bomb radiocarbon signal were not recorded before 1970 and a much sharper rise.

Discussion

Application of the bomb radiocarbon technique to the vertebrae of shortfin mako has demonstrated its utility as an age validation tool for this species. The bomb radiocarbon signal measured in the shortfin mako was temporally similar to the records observed in western North Atlantic Ocean bivalves and fish (Weidman and Jones 1993; Campana 1997), although more comparable to the slightly out-of-phase record determined for the porbeagle (Campana et al. 2002). Records from water samples (Nydal et al. 1998) and corals (Druffel and Linick 1978; Druffel 1980, 1995; Guilderson et al. 1998) show a synchronous rise in radiocarbon levels in the late 1950s to the early 1960s, though the years of peak differ depending on the oceanography and depth of sampling. For fishes, most records have been from teleosts and followed the same trend (Kalish 1993; Campana 1997; Campana and Jones 1998; Kalish et al. 2001; Kerr et al. 2004). For elasmobranchs, one possible exception is with the school shark, *Galeorhinus galeus*, from the western South Pacific Ocean (Kalish and Johnston 2001); the first effects of the bomb radiocarbon signal may have appeared in 1979, more than 15 years after the onset recorded in otoliths from the same region (Kalish 1993). This was attributed to underestimation of age.

The dietary source of carbon for the shortfin mako, combined with slight underageing, could be responsible for the phase shift in the bomb radiocarbon signal and some of the unusually low levels (Campana et al. 2002; Kerr et al. this issue). The source of carbon in elasmobranch noncalcified tissue comes from the diet (Fry 1988; Campana et al. 2002). The incorporation of this carbon in the vertebrae carries the signature of the prey and may be generally older than the surrounding water because of a trophic level delay. This effect may be more evident in larger prey because radiocarbon is carried through more trophic levels. Therefore, large sharks may have incorporated a more delayed signal because they often feed on larger prey (Stillwell and Kohler 1982). The four samples showing more of a phase-lag were taken from growth bands formed at an older age (age 9–18), hence a slight depletion in radiocarbon could explain the discrepancy.

The $\Delta^{14}C$ levels from three samples are among the lowest recorded for the pre-bomb period in the western North Atlantic Ocean. These values are about twice as low as the pre-bomb $\Delta^{14}C$ levels from other regional marine organisms and water samples, which range between –40‰ and –80‰ (Druffel 1989; Campana 1997; Campana and Jones 1998; Nydal et al. 1998; Baker and Wilson 2001; Kalish et al. 2001). Only the porbeagle has pre-bomb values more depleted than corals and fishes in the western North Atlantic Ocean (as low as –114‰; Campana et al. 2002). These depleted levels can be explained based on a diet of prey that live in waters deeper than the mixed layer, depths where the radiocarbon is depleted, relative to surface waters (Broeker et al. 1985; Kalish 2001).

Movement and feeding studies support the notion that an increase in the variability of the source of radiocarbon could partially explain the phase lag observed in some samples. Analyses of feeding habits and tracking studies indicated deep-water squid were a component of the shortfin mako diet in the western North Atlantic Ocean (Carey et al. 1978; Stillwell and Kohler 1982). Tracking studies in the eastern North Pacific Ocean indicated young shortfin mako (up to 1.7–1.8 m TL) frequent the upper 50 m of the water column (corresponding to the 18–20°C range), but make excursions to deeper waters, presumably to feed (Holts and Bedford 1993; Klimley et al. 2002; Sepulveda et al. 2004).

Although dietary effects can explain some of the variation, there is no empirical evidence to rule out some degree of metabolic reworking. Based on ^{210}Pb distributions within vertebrae, Welden et al. (1987) determined that the inorganic component in shark vertebrae may be metabolically unstable. The within-shark $\Delta^{14}C$ signal for the adult shortfin makos that lived through the pre-bomb to post bomb era, however, indicated there is strong evidence that the organic carbon is conserved to a significant extent. Otherwise, no recorded increase with time would be evident and the distribution of pre- and post-bomb values would likely be randomly distributed. The observed variability within this general trend, however, could be due to either minor differences in sample extraction or differences in localized growth and deposition. This notion is

supported by the different measured $\Delta^{14}C$ levels in the sample that was similar in vertebral location to one analyzed by Campana et al. (2002) and similar findings were recorded for the white shark (Kerr et al. this issue). However, the samples from Campana et al. (2002) were not demineralized prior to radiocarbon analysis.

The geographic location of an individual shark during a particular period of its life can also introduce further variability in the radiocarbon signal. Follows and Marshall's (1996) model, consistent with the observed patterns, indicated there was an excess of bomb ^{14}C in the western part of the North Atlantic Ocean basin, due to enhanced eddy stirring in the western region. Results of a study on movements of 231 shortfin mako sharks in the western North Atlantic Ocean indicated that 31 (13.4%) sharks recaptured were caught after traveling distances exceeding 1000 nautical miles (Casey and Kohler 1992). One of the sharks tagged off the northeastern United States was recaptured off the coast of Spain, after a straight-line journey of 2452 nautical miles. Because shortfin mako are highly migratory, exposure to prey in different regions might play a role in the variable radiocarbon levels seen here.

The results of this work support the annual band-pair interpretation for western North Atlantic shortfin mako aged up to 31 years, but does not rule out the early age findings for biannual band-pair deposition. The biannual band-pair interpretation could be valid for the first few years of growth, as was indicated by length-frequency and tag/recapture data (Pratt and Casey 1983). However, extrapolation of the early growth pattern to older ages is not supported by the findings of this study.

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